A COMPARATIVE REVIEW OF THE AMPHIBIAN FAUNAS OF SOUTH AFRICA AND MADAGASCAR, WITH SOME SUGGESTIONS REGARDING THEIR FORMER LINES OF DISPERSAL.

By John Hewitt, B.A. (Cantab.).

Since the publication of the British Museum Catalogue of Batrachia Salientia several important additions have been made to our knowledge of the amphibian fauna of South Africa: these are incorporated in my paper on the South African Batrachia in the Records of the Albany Museum, Vol. 2, No. 3; and in a recent paper, Nouv. Archiv. du Museum d'Hist. Nat., Paris, 1909, Dr. F. Mocquard gives a complete list of the Batrachia of Madagascar. These lists seemed to offer a favourable opportunity for examining the known facts of distribution in terms of certain modern theories on the past configuration of the earth's surface. Those theories may be briefly stated as follows: From geological considerations it is believed that in Permian times a large Indo-oceanic continent connected together Australia, India, Madagascar, the Seychelles and southern Africa, and these connections persisted as late as the Upper Cretaceous period, but were broken up into islands at an early tertiary date: the derite connection between Australia and South Africa disappeared first, but Dr. Schönland believes, on botanical evidence, that it was still in existence during Lower Cretaceous times (see Trans. S. Afric. Phil. Soc., 18. 3., p. 321): the land connection between Madagascar and India persisted until the Eocene period, or perhaps considerably later as an archipelago, and there is abundant zoological evidence that the union between Madagascar and southern Africa is also of recent date, and indeed as a series of swamps may even have continued into the early Pliocene. On the other hand, from similar considerations it is hardly less certain that an extensive land connection has existed between the neotropical region and West Africa during the later secondary and early tertiary periods. Contemporaneous with these far-reaching land bridges across the Atlantic and Indian Oceans of the later secondary period, a great sea, perhaps dotted with islands, stretched north of the Equator from Panama by way of Africa as far as southern Asia, and thus the southern land-mass which included southern Africa and Madagascar was quite cut off from the palaearctic region. At that time the fauna of this large land-mass would have much in common throughout large areas, without being absolutely homogeneous, but after the separation of Madagascar and the formation of the African continent in its present shape, a new fauna coming from the palaearctic region arrived in South Africa, but was unable to reach Madagascar by this time an island. The present-day fauna of Madagascar should therefore be of particular interest, as it preserves, with but little admixture of foreign forms, the

descendants of a fauna which was probably common to the whole of the southern Ethiopian region in early tertiary times: moreover, it is the only large portion of that vast area which has been thus isolated from the world. Unfortunately, however, there is a great lack of palaeontological data with which to supplement and check the deductions which we may draw from the present-day Malagasy fauna. The published lists of that fauna reveal the fact that the main groups of vertebrata are represented in Madagascar by an unusually small number of forms, and these are often of ancient type; for instance, amongst reptiles there are no Lacertidae, no Agamidae, and no Varanidae; there are no viperine nor proteroglyphous snakes, and of freshwater fish, according to Mr. Boulenger, there are only sixteen species. These facts seem to indicate that the larger Ethiopian area of the early tertiary period was correspondingly poor in present day types.

As regards the relationships of the Madagascar fauna of to-day, we know that it is for the most part Ethiopian and that also there are a few Indian and American types, but it is to be regretted that only in a few groups of animals have these various relationships been submitted to a thoroughly critical examination. A very suggestive inquiry into the affinities of the sub-fossil Lemuridae of Madagascar has been recently published by Dr. Standing (Trans. Zool. Soc., Vol. 18, No. 2). Some of his conclusions, which are of interest to us from our present point of view, are as follows: "In the main the affinities of the Malagasy fossils are with the primates of South America, but nevertheless there are certain features which find their closest analogy in various old-world forms"; "the incisors of Archaeolemur (of Madagascar) are almost identical with those of various African genera"; and "the various genera of the Lemuridae and the new-world monkeys seem to be survivals of the primate stock formerly inhabiting the ancient southern land-mass which included South America, Madagascar and a part at least of South Africa and India": and he concludes that in giving rise to the Malagasy lemurs, this early primate stock, as a result of isolation being removed from competition with the dominant mammalian groups which spread over other parts of the world, experienced an arrest of brain development and perhaps even a retrogressive evolution: and lastly, it is no longer possible to separate primates into the two sub-orders Anthropoidea and Lemuroidea. In the same work Dr. Elliot Smith writes: "the brain features of the Prosimiae are very uniform", and the larger species of Galaginae have a type of brain almost identical with that of the Lemuridae, whilst Garnett's Galago and Loris have many brain features in common"; and further "in Propithecus, Lemur, Loris, Tarsius, the Hapalidae, and the Cebidae there is a complete series of transitional stages leading up to the conditions met with in the old-world apes and man". This investigation clearly reveals the fundamental affinity of the Lemuridae with the American monkeys, but it is important to note that there is a still closer affinity between certain elements of the Malagasy and South African faunas as shown in the sub-family Galaginae.

The case of the Madagascar boine snakes, which are generally supposed to be of pronounced American relationship, has been dealt with

by Mr. Beddard in the Proceedings of the Zoological Society, with results which are somewhat unexpected : for, he says, there are important anatomical differences between the Madagascar species of Corallus and Pelophilus and the American snakes which have been referred to the same genera, the former being in some respects more in agreement with the old-world pythons, and he considers that it is not now desirable to subdivide the Boidae into the usually accepted groups of Boinae and Pythoninae. This case is an illustration of the obvious fact that it is unsafe to gauge generic relationships by means of superficial characters.

The only important facts to be added to the known data concerning the South African frogs relate to the genera Heleophryne and Cacosternum : the former, as I have shown (Annals Transvaal Museum, Vol. 2, p. 45), really belongs to the Cystignathidae, and the latter, which was first assigned to the Ranidae and more recently to the Engystomatidae, appears to me to be more correctly placed in the Dyscophidae (or sub-family Dyscophinae of Gadow), as the upper jaw is undoubtedly provided with teeth.

The amphibian faunas of South Africa and Madagascar are composed as follows :—

	SOUTH AFRICA.	MADAGASCAR.
Aglossa	Xenopus 1	—
Bufonidae	Bufo 8	—
Cystignathidae	Heleophryne 2	—
Ranidae	Rana 15, Chiromantis 1, Cassina 1, Hylambates 3, Rappia 9, Megalixalus 2, Arthroleptis 2, Phrynobatrachus 1	Rana 2, Rhacophorus 21, Rappia 6, Megalixalus 3, Mantidactylus 23, Arthroleptis 1.
Ranidae, sub-family *Dendrobatinae*	—	Two peculiar genera.
Engystomatidae, sub-family *Engystomatinae*	Hemisus 2, Breviceps 5, Phrynomantis 1	Calophrynus and three peculiar genera.
Engystomatidae, sub-family *Dyscophinae*	Cacosternum 1	Nine peculiar genera.

Aglossa.

Xenopus laevis.—The genus ranges through tropical and South Africa, but is absent from North Africa : the genus Pipa of the Guianas is closely related to Xenopus, and Hymenochirus of Equatorial Africa is stated to be in some respects intermediate between the two genera. As this sub-order is absent from Madagascar and the oriental region it would seem likely that the original home was in the neotropical region and that Xenopus is comparatively new to Africa.

Phaneroglossa.

Bufonidae.—There are about seven species of Bufo in the South African region, the commonest being *B. regularis*, which occurs throughout

the whole of Africa with the exception of Barbary: probably the only species peculiar to South Africa are angusticeps, vertebralis, and granti, the latter perhaps only a variety of angusticeps. The genus is cosmopolitan with the exception of Madagascar and Australia, from which latter fact Gadow concludes that the original centre of the genus Bufo was not in Notogaea,* though the neotropical region is at the present day richest in number of species: however this may be, we are safe in regarding the genus as comparatively new to Africa on account of its absence from Madagascar and from the fact that Africa has no peculiar genera of Bufonidae. The only other Bufonid genus occurring in Africa is Nectophryne of the Cameroons, Gaboon, and East Africa, the same genus having a number of representatives in southern Asia, especially Borneo. The other genera of the Bufonidae are mainly distributed between the neotropical region and Australia, and, though there may be some doubt about the place of origin of the genus Bufo, it is very probable that the general Bufonid stock arose in Notogaea. I believe therefore that the genera Bufo and Nectophryne arrived in Africa at a comparatively recent date, travelling from the neotropical region via West Africa: that this was the direction of the migration, rather than from east to west, I assume from the fact of the absence of Bufo in the Australian region. The distribution of these genera suggests that they arrived in the Ethiopian region at a time when the Indo-Oceanic continent had already been reduced by the northwardly advancing ocean to a narrow strip extending from East Africa to Asia, the island of Madagascar being by this time separated from its continent.

Cystignathidae.

As I have already stated, the genus Heleophryne of Mr. W. L. Sclater is really a Cystignathid. This family is otherwise confined to Australia and South America, and on the whole I think the South African genus is more closely related to the Australian section: this conclusion is mainly arrived at from consideration of the somewhat dilated sacral diapophyses, though in its Y-shaped terminal phalanges it is at once distinguished from all Australian genera. But to explain its occurrence at the southern extremity of Africa is no simple matter, for, whilst its structural peculiarities indicate that it is not an accidental immigrant of very recent date, it is believed that the Anura are a comparatively newly developed group of animals—Dr. Gadow says that the earliest known fossils are scarcely older than the Middle Eocene—whereas the direct connection of South Africa with Australia was probably severed at a very early date, at any rate not persisting beyond Cretaceous times. However, as regards the age of the Anura, an estimate based only on the palaeontological evidence may be very unreliable considering the extreme scantiness of the record, and therefore our conceptions of their antiquity must be based largely on the facts of present-day distribution viewed in the light of our knowledge on the past changes of land and sea over the

* The terms Notogaea and Arctogaea (southern and northern world) are here employed in the same sense as by Gadow in the Cambridge "Natural History", Notogaea comprising the Australian and neotropical regions of Sclater.

earth's surface: this is not a circular argument, as the evidence for these latter hypotheses is based on sound geological facts. The very fact of the occurrence of the two main branches of the Cystignathidae in Australia and South America respectively is sufficient to imply the existence of this family in Cretaceous times, for according to all accounts the land connections between those two countries must have terminated by early tertiary times at the latest. At the same time we must add that the Cystignathidae is perhaps the oldest family of the Anura.

Again, it is obvious that the immigration of Australian types into southern Africa can be dated less remotely the more northward the place of entry. Now, even the present-day distribution of this genus is very imperfectly known: it was first taken in the Stellenbosch neighbourhood and recently at Knysna, but as apparently it is of purely arboreal habit it must easily escape notice, and we may reasonably expect that it will prove to have a much wider range: very likely the genus will be found to occur in the forest region of the whole coastal strip of Cape Province at least. Nevertheless, it should be mentioned that from analogy with the plants, the western portion of Cape Province is just the locality where we might have expected to meet with Australian types, for Dr. Schönland says: "It is certainly most extraordinary that wherever we find the closest agreement between the floras of the two countries (South Africa and Australasia), it is between the boxed-up flora of the Cape Province (of botanists, i.e. south-west Cape Colony) and the flora of Australia, chiefly west and south-west Australia, and when we consider that this connection exists in widely separated orders these facts become all the more wonderful." But even from a botanical point of view it seems necessary to postulate a former wider distribution in South Africa for this particular flora, and in the same paper we read: "A former eastward extension (of the typical Cape flora) is certainly demanded by our theory . . .; we know that even now many outliers of the typical Cape flora reach far east, and their number would probably be much greater if the tropical African flora did not appear as a formidable competitor in the coast regions." In this connection I may remark that the various botanical areas of South Africa have little significance from the point of view of vertebrate zoology: it is quite true indeed that the peculiar South African element is specially concentrated in south-western Cape Province, but thence it is diffused all over southern Africa, the Congo basin excepted, and only two areas, an eastern and a western separated by the Drakensberg Range, have any claim even to sub-regional rank, though within a sub-region the several species of a genus may range themselves according to the various environmental conditions. Amongst the South African reptiles perhaps the most striking case of Australian relationship is that of the genus Oedura, which is confined to the South African and Australian regions. The distribution of our species is as follows: *O. africana*,* Damaraland, eastern Cape Colony, Natal: *O. nivaria*, first taken in Natal at the highest point of the Drakensberg Range and more recently in the Pirie Bush (F. A. O. Pym). The case of Oedura will

* The Damaraland record is open to suspicion: nivaria is probably a synonym of africana.

therefore favour the supposition I have made for an extension in a north-easterly direction of the distribution area of Heleophryne. Lastly, in the arboreal habit of this frog we have another possible clue to the problem, for granting that in Upper Cretaceous times the direct connection between South Africa and Australia had largely disappeared, yet stepping-stones in the form of a chain of sinking islands affording opportunity for the dispersal of some arboreal creatures only, may still have existed.

Ranidae.

The whole family of Ranidae is distributed as follows:—Ceratobatrachus, which has teeth in both jaws, is known only from the Solomon Islands: the Raninae, which have teeth only in the upper jaw, belong almost entirely to Arctogaea, and except for the genus Rana, which ranges throughout the whole region, are limited mainly to tropical and sub-tropical areas: the Dendrobatinae, which are characterized by an entire absence of teeth, occur in Madagascar, Gabun, and the neotropical region.

The genera of Raninae (Ranidae of many authors) fall into two sections according to the presence or absence of supernumerary digital phalanges, the former section comprising the following genera:—Chiromantis, Cassina, and Hylambates, which belong to tropical and South Africa, Rothschildia of Abyssinia, Rappia and Megalixalus occurring in tropical and South Africa and Madagascar, with an odd species of the latter genus in the Seychelles, Rhacophorus of Madagascar, India, Malaya, and Japan, Mantidactylus of Madagascar, Ixalus of India and Malaya, Nyctixalus of East Indies, Phrynoderma of Burmah, and Chirixalus of the Karin Hills. Dr. Gadow says "it is doubtful if all these genera are thereby more nearly related to each other than to the rest of the Raninae", but as the African members—with the possible exception of Chiromantis—seem to be more closely related to each other than to Rana, and as the distribution of the whole section is very suggestive of a former continuity through the Indo-Oceanic continent, I am regarding them as a natural group, and, as will be explained later, I suspect that this is the older section of the family. The other section of the Ranidae, comprising genera which are without supernumerary digital phalanges, occurs throughout Arctogaea and the tropics of both worlds, and has the following genera in South Africa:—Rana, Arthroleptis, and Phrynobatrachus, in addition to which there are one or two monotypic genera in tropical Africa, for instance, Phrynopsis of Mozambique: these genera, with the exception of Rana with its fifteen species in South Africa out of a total of about 150 species which range throughout the whole tropical and temperate Arctogaea, hardly penetrating into Notogaea, and Arthroleptis which has an odd species in Nossi Bé (with a generic ally in the Seychelles) are peculiar to the African continent: on the other hand, Madagascar has no peculiar genus belonging to this section, and indeed its only representatives are two species of Rana—one of them being the *R. mascariensis*, widely distributed in tropical and South Africa—and the single species of Arthroleptis, which, however, appears to be confined to Nossi Bé. It is possible therefore that the Madagascar representatives of this section are merely straggling immigrants of quite recent date, and we can be sure that this island was outside the area of evolution of the

genus Rana and the various genera which are minus the supernumerary phalanges. But to return to the other section, this is strongly developed in Madagascar, and although three out of the four genera occur elsewhere, the whole section is no doubt truly endemic there, as indicated by the large peculiar genus Mantidactylus and the marked development of the genus Rhacophorus. Two of the genera Rappia and Megalixalus are common to South Africa and Madagascar, whilst the genus Rhacophorus has many species both in Madagascar and the Indian region, but these facts do not necessarily imply a specially great antiquity for such genera, as, being of arboreal habit, like the great majority of the members of the same section, they would no doubt be able to effect their continuous dispersal during the greater part of the time when the direct land connections were dissolving and under conditions which would altogether isolate terrestrial or purely aquatic frogs which unanimously abhor salt water. Somewhat parallel instances amongst mammals are known, and Dr. Standing explains the occurrence in Madagascar of such late forms as pigs and hippopotami, and the absence of other groups which are known to have existed on the African continent at an earlier date, on the hypothesis that Madagascar and Africa have remained in connection up to a very late tertiary date by means of a low-lying isthmus covered with dense jungle and intersected by swampy tracts: this would offer but little obstacle to wild pig, but would be a complete barrier to almost all other mammals except purely arboreal forms.

As Dr. Gadow has pointed out, the entire sub-family of Raninae is in its fulness and diversity of development essentially palaeotropical; from which we may infer that its centre of origin was the great Indo-Oceanic continent, and I believe that the arboreal section of Madagascar and South Africa represents the original stock without much modification—but this is a point for anatomical investigation. As already mentioned, the African members of the other section, the genus Rana excepted, are all peculiar to the region so that they were probably developed in this continent: several of them have near allies in eastern Asia, e.g. Phrynobatrachus and Arthroleptis appear to be closely related to Oreobatrachus from Mount Kina Balu in Borneo, whilst Cornufer of Austro-Malaya and Polynesia has a very near ally in Petropedetes of the Cameroons and Gabun. The land connections which are implied in these relationships were presumably in existence subsequent to the isolation of the main island of Madagascar. It should be added also that there are a few Ranid genera in tropical South America and Central America: this assembly seems to be a natural one, but its relationships are unknown to me. I judge from the distribution that they come from the old world by way of the transatlantic bridge.

As regards the genus Rana, its distribution suggests an old-world origin, and in the new world it appears likely that it travelled from the North to South America: if we suppose that it had its origin in Africa, it must be understood that this could only have happened subsequent to the dissolution of the transatlantic land bridge.

Probably the most distinctive section of this large and widely dispersed genus is that which was formerly included under the generic name

Pyxicephalus (*R. adspersa, delalandi, natalensis*, etc.,) and it is a noteworthy fact that this section (as understood by Nieden) is confined to tropical and South Africa, with an odd species in Madagascar, from which we may conclude that Pyxicephalus really is endemic in this region. Although in some of its characters it is no doubt very specialized, yet on the whole I think Pyxicephalus is more primitive than the ordinary type of Rana: for instance, whereas in Rana the metatarsals are separated by web, this is not the case in Pyxicephalus, the condition in Rana being no doubt a secondary adaptation character. There is therefore some justification for the supposition that the genus Rana arose on the African continent. Fossil Ranidae are recorded from the Eocene of India (Oxylossus) and from the lower Miocene of Germany (Rana).

The sub-family Dendrobatinae (Dendrobatidae of some authors) has two genera in Madagascar, Nossi Bé and Reunion, one in French Congo, and one in South America. They appear to differ from Raninae only in the absence of teeth, and Gadow therefore questions if they really constitute a natural group. In the absence of certain evidence on this point we cannot make use of their distribution data: it is important to note, however, that parallel facts of distribution are known in other groups of vertebrates.

Engystomatidae.

The most typical section of this family is the sub-family Engystomatinae. The South African genera Hemisus and Breviceps are confined to tropical and South Africa whilst the third genus, Phrynomantis, has also a representative in the island of Amboina. It is worthy of note that in Africa this genus properly belongs to the tropical region, ranging from Gold Coast and Angola to German East Africa, and extending southwards into the sub-tropical portions of our area, but not reaching Cape Province (Phrynomantis occurs at Kimberley, but Miss Wilman believes that it is an accidental introduction along with mine timber.) Madagascar has four genera, of which three are peculiar, whilst the fourth, Calophrynus, has other species in Borneo, Burmah, and South China. The whole subfamily is distributed as follows: Tropical and South America, seven genera; Africa three; Madagascar four; India and Malay region, especially New Guinea, thirteen. The inter-relationships of these various genera are unknown to me. The sub-family Dyscophinae includes about ten genera, which are all confined to Madagascar, with the exception of Calluella in Burmah, Colpoglossus in Borneo, and Cacosternum in Africa. The genus Cacosternum differs, however, from all other Dyscophinae except Anodontohyla in the absence of palatine teeth, and as the precoracoids also are absent, it must be counted as a degenerate member of the sub-family and a connecting link with the Engystomatinae. As this sub-family constitutes the more primitive section of the Engystomatidae, we may surmise that the original home of the family was in the Indo-Oceanic region, an assumption which is in agreement with the present-day distribution of the Engystomatinae: and seeing that these genera as a whole are slow of movement, their more extended distribution in South America would seem to indicate that the Engystomatinae are not so recent as the Raninae.

We may now very briefly mention the distribution of those families of Anura which do not occur in South Africa nor in Madagascar.

The Hylidae have their headquarters in South America, but they occur also in North America and in Papuasia, whilst a few stragglers of the genus Hyla extend from America throughout the palearctic region, southwards into southern China and northern India, and though absent from the Malay region (except New Guinea), there are several species of Hyla in Australia. It appears therefore that, roughly speaking, Hylidae occur in every habitable part of the globe excepting the great Indo-Oceanic region as it was immediately subsequent to its separation from Australia. The distribution records suggest, that in passing between the old and new worlds the genera Hyla and Rana made use of the same land connections (probably across Bering Straits), but travelled in opposite directions.

The Discoglossidae occur in the palaearctic region, North America, and in New Zealand, and are recorded from middle and upper Miocene of Europe, whilst the Pelobatidae occur in North America, Europe, India, Ceylon, Malaya, and New Guinea.

The distribution of the Apoda is particularly interesting from our present point of view. These worm-like creatures, which are entirely restricted to a burrowing life in damp ground, must have exceedingly limited opportunities for dispersal. Major Alcock (A.M.N.H., 1904, p. 267) gives the following list:—Out of a total of eighteen genera, tropical America has nine genera (seven peculiar) comprised in twenty-eight species, West Africa has four genera (two peculiar) with five species, East Africa has five genera (four peculiar) with five species, the Seychelles have three genera (two peculiar) with four species, and there are four genera (two peculiar) comprised in six species in India and South-East Asia. One genus, Dermophis, is common to tropical America, West and East Africa, the genus Hypogeophis is common to East Africa and the Seychelles, Herpele occurs in tropical America, West Africa, and Cachar (India), and the genus Uraeotyphlus is known only from Gabun and Malabar. It appears that in Africa the Apoda are confined to a broad belt of country stretching from east to west in the Equatorial region, and are absent altogether from South Africa, Angola, and Mozambique. Considering the preponderance of genera and species in the neotropical region it seems highly probable that this was the original home of the group and that like Xenopus, Bufo, and Nectophryne, the Apoda reached the Ethiopian region subsequent to the separation of Madagascar: and it is evident that after Madagascar had attained an insular position there still remained for some time a land-bridge stretching from East Africa to the Indian region and including the Seychelles.

In the Proc. Zool. Soc. for 1905, p. 191, there is a very interesting paper by Dr. Gadow on the Mexican Reptiles and Amphibia, where he gives an outline of the present and past distribution of the Anura families in that part of the world. This has an important bearing on our present question, and I therefore give a brief summary of some of the salient facts therein stated. During Cretaceous times Central America and Mexico were covered by sea, and even by the end of the Eocene period North and South America were still completely separated: during Miocene times,

however, extensive land connections stretched between North and South America, and the Greater Antilles were united with Mexico and Central America: but at the end of the Miocene the geographical relations of that part of the world were much the same as to-day, and no profound changes have occurred since. It follows therefore that some very important deductions can be made by comparison of the Mexican fauna with that of the Antilles. The facts are:—

Cystignathidae, extending from their South American centre into Mexico and the Antilles, but not occurring in the United States.

Hylidae, well represented in South America, Mexico, and Antilles, and extending throughout North America.

Bufonidae: Central America and Mexico are one of the centres of this family, and it extends into the Antilles.

Engystomatidae, well represented in South America, occurring in Mexico, a few in North America, but none in the Antilles.

Ranidae: a number of peculiar genera in the north-west portion of South America, but in Mexico and North America only the genus Rana occurs and there are none in the Antilles.

Pelobatidae, extending from North America into Mexico, but not reaching Central America nor the Antilles.

Apoda: they occur in South America and in Mexico, but are not known from the Antilles.

From consideration of the Ranidae and Engystomatidae it will be seen that the transatlantic bridge could not have included the Greater Antilles, and in fact it must have been appreciably south of that region. And if we suppose that the transatlantic connection as a complete bridge came to an end at an earlier date than the Antillean land connection, at the same time making due allowance for the great length of the former, it can easily be shown that all these facts of distribution are in accordance with the speculations made in this paper concerning the place of origin and the migrations of the various Anura families. The absence of the Ranidae and Engystomatidae from the Antilles is quite comprehensible when we regard them as old-world families which crossed over to the neotropical region at a time when the land-bridge was just beginning to give way, and when eventually they had travelled northwards as far as the Antillean bridge this was no longer complete. That Bufonidae, Hylidae, and Cystignathidae occur in the Antilles is what we should expect of groups which are American in origin, but whereas the Bufonidae have been able to avail themselves of the transatlantic bridge, this is not the case with the other two families: the explanation no doubt lies in the fact that the Cystignathidae and probably also the Hylidae had their centre of origin far south, perhaps in the great land area lying between Australasia and South America, and by the time they had advanced northwards into the transatlantic bridge, this had begun to break up, whereas in the case of the Bufonidae the American terminus of that bridge was probably nearer their centre of origin.

The various tertiary land connections of the Ethiopian region as indicated in this paper do not furnish a complete explanation of all the distribution data: it is difficult to understand, for instance, why such

widespreading forms as Nectophryne and the Apoda have not extended further southwards in Africa and why the Dendrobatidae have such a disconnected distribution. To explain the paucity in Madagascar of early African mammals, Tullberg (whose paper I have not actually seen) suggested that the east part of Africa, along with Madagascar, had been separated by an arm of sea from the main south-western African mass, and not until after the isolation of Madagascar (about late Oligocene) were the two portions of Africa united, at which time East Africa was probably united to South-West Asia by a continuous land-bridge along which the Proboscidea reached India. There is much to be said in favour of this view if we include in the eastern section of Eocene times the whole of Sclater's Cape Province with Madagascar, as it well explains the distinctness of that Province and its fundamental relationships with Madagascar. In such case there may have been various transitory connections between the separated areas, some of which would be the means of introducing certain American types which were shortly afterwards isolated in Madagascar.

In concluding this short paper, it must be admitted that the kind of evidence that is required to properly establish these hypotheses is altogether lacking, in the almost complete absence of fossil forms : nor do we possess the whole evidence of comparative anatomy, for our judgments of generic relationships are based upon the more easily ascertained and superficial characters, and the data for a genetic arrangement of the genera are still wanting. Mocquard points out that in the Arcifera, especially the Hylidae, there are two sections parallel to those of the Raninae, so that it is even possible, though I think not probable, that our whole classificatory arrangement will have to be altered accordingly. The available facts certainly show how unsatisfactory must be any rigid arrangement of the world's surface into zoological regions, seeing that the fauna of any large area is a heterogeneous assembly of species which have varied origin and history.